

THE STATUS OF THE GENERAL SYSTEM OF CLASSIFICATION OF FLOWERING PLANTS¹

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INTRODUCTION

The Linnaean system of plant classification, which arranged all the genera into some 24 admittedly artificial classes, was such a great improvement over its predecessors, and was so universally adopted, that eventually it outlived its usefulness and became a handicap to further taxonomic progress. In the 9th decade after the appearance of the *Species Plantarum*, distinguished botanists such as W. J. Hooker (1) in England and Amos Eaton (2) in America were lamely defending their continued use of the familiar Linnaean system, instead of one of the several purportedly natural systems that had been put forward in its place. Within another few years the Linnaean system simply vanished.

The well known and very useful Englerian system is having a similar history. Now moribund, it continues to be used because people are familiar with it, and because there is as yet no agreement on a successor. The most recent [1964] edition of the Engler Syllabus (3) is noteworthy, among other respects, in that it marks the recognition in Engler's home institution that his system must be so extensively modified as to lose its identity. The monocots are placed after the dicots in this edition and are completely reorganized, with the *Alismataceae* coming first in the sequence. Only a few families of dicots, such as the *Cactaceae* and *Curcubitaceae*, are moved far from their accustomed place, but there are numerous notes indicating that a change in the position of this or that family will be necessary in order to associate it with its nearest relatives. Abandonment of the *Amentiferae* and recognition of the Ranalian complex as the primitive group in the angiosperms are clearly forecast in this edition of the Syllabus.

The critical weakness of the Englerian system is that it fails to recognize the significance of reduction and therefore tends to equate the simple with the primitive. As a result, the *Amentiferae* are considered to be primitive among the dicots, and the *Typhaceae* among the monocots, and no real connection is seen between the monocots and dicots. By 1926 Engler (4) had realized that the flowers of the *Amentiferae* are simplified rather than primitively simple, and he argued that their extreme reduction indicated the great antiquity of the group. Such an argument misses the whole point of a phylogenetic system. An essential requirement of any phylogenetic system is that one start with the groups which are least modified from the ancestral prototype, rather than with those that have undergone the most change. All groups are of equal age, if one takes in all the ancestors as well as the members of the group. It is only if one bases concepts of age on the members that

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would actually be referred to a particular group that groups differ in age and a phylogenetic system becomes possible.

We should note at this point that the now widespread dissatisfaction with the Englerian system does not relate primarily to the arrangement of genera into families. Some disagreement on the limits of families is inevitable, and the problem of lumping or splitting will always be with us, but no one wants to reshuffle the genera into a basically different set of families. The dissatisfaction relates instead to the arrangement of families into orders, and to the concepts of relationships among the orders, including how these may best be arranged in a linear sequence. Such arrangements necessarily depend to a large extent on one's concepts of the nature of the primitive angiosperms and the evolutionary trends that have affected the structure and chemistry of their decedents.

SIGNIFICANCE OF THE FOSSIL RECORD

One of the greatest problems in any consideration of the evolutionary relationships among the angiosperms and the ancestry of the group is that the fossil record tells us so little. So far as the fossil record is concerned the angiosperms might have originated by special creation early in the Cretaceous period as a set of several woody families occurring in various parts of the world and having no connections to any other groups. Several Jurassic and Triassic fossils have at one time or another been considered to be possibly angiospermous, but some of these have been shown to be gymnospermous, and the others are doubtful at best (5).

Perhaps the most interesting preCretaceous fossil that might prove to be an angiosperm is *Sanmiguelia* (6), a palm-like plant from Triassic deposits in Colorado. The fossils consist only of leaf-impressions, with no cellular detail. They do indeed look like parts of palm leaves, and if they had been found in Cretaceous or later deposits they would probably pass as palms without serious question. However, they are also much like cycadophyte leaves, and if there were no such things as palm trees these fossils would doubtless be considered to be cycadophytes. Palms are not usually considered to be very primitive among the angiosperms; indeed they are one of the more highly specialized groups. If *Sanmiguelia* is really a palm, some re-thinking of our concepts may be in order, but without flowers, fruit or wood its status as a palm must rank as an interesting possibility rather than a fact or even a probability.

The question of the affinities of *Sanmiguelia* points up one of the most pervasive problems in the study of fossil angiosperms. Aside from pollen grains, most of these fossils are mere leaf-impressions. Fruits, when present, are seldom attached to the leafy branches and rarely show enough structural detail to be identified without a great deal of inference, although a few kinds, such as the double samaras of maples, are easy enough to recognize. Fossil flowers are rare and do not generally show the structures needed for accurate identification. Students of vertebrates are fortunate in that the parts most likely to be fossilized (the bones) are also the parts that tell the most about the nature and taxonomic affinity of the animal. Angiosperm taxonomists are in the reverse position. The parts most likely to be

fossilized (leaves) tell us little that can be relied on. All taxonomists are aware of the difficulty of identifying sterile material, and the difficulty is compounded when one has not the plant itself, but merely an imprint of part of it. A purported fossil cactus was recently reinterpreted as the rhizome of a member of the *Cyperaceae* (7), and a long list of equally startling reinterpretations could be cited.

Even when an angiosperm fossil can be satisfactorily identified, it merely documents the existence of a particular group at a particular time. The vegetative diversity among and within the families of angiosperms is far too great, and too bewildering, to permit accurate recognition, on vegetative characters, of forms transitional between the modern groups. Some Cretaceous leaf-impressions of *Sassafras* are so characteristic that it is hard to question their identity, but what do these fossils tell us about the relationships of *Sassafras*? Nothing.

Pollen grains, both modern and fossil, can often be identified, at least to the family, more accurately than leaves. A great deal of information about fossil pollen has now been accumulated, but most of it is locked away in the files of oil companies and is not readily available to the scientific fraternity. From Elso Barghoorn (5, 8) I learn that much of the older fossil angiosperm pollen cannot be certainly assigned to any existing family, and that pollen which can be identified as representing herbaceous families is virtually nonexistent before the Miocene period. Even such wind-pollinated groups as the *Chenopodiaceae* and some of the *Compositae* do not show up until the Miocene, and the presence of herbaceous pollen is now coming to be looked on as a marker of Miocene or post-Miocene deposits. This is in accord with conclusion which most taxonomists have accepted on other grounds that the herbaceous habit in angiosperms is secondary rather than primitive.

Since the fossil record tells us so little, our concepts of relationships among the angiosperms must be based largely on comparisons of living species. This does not put us in so difficult a position as one might imagine. It is becoming increasingly plain that the number of potential schemes which will adequately provide even for the information now available, without serious internal contradictions, is not large; and the range of choice becomes increasingly more restricted as more information becomes available. It is the now obvious contradictions in the Englerian system which have stimulated botanists to strive to create a better one. New information is needed to help solve many of the problems, but even the presently available evidence imposes narrow limits on the range of potentially acceptable schemes, and no scheme has yet been devised which properly provides for all the information now available.

ANCESTRY OF THE ANGIOSPERMS

Before getting to the main business of the general system itself, we might profitably consider the probable ancestry of the angiosperms. Here in our discussion we are faced with the common pedagogical dilemma that everything ought to come before everything else. Our thoughts on the ancestry of the angiosperms are necessarily conditioned to some extent by our beliefs on the relationships and evolutionary trends within the group. A potential ancestor should be something from which

the primitive characters within the angiosperms could reasonably have been derived, and the possible connection to the angiosperms should be with the more primitive families rather than with the more advanced ones.

Modern thinking on the ancestry of the angiosperms is based on what we might call the Randalian concept of angiosperm evolution, to which we will refer again after a bit. The difficulties in finding a potential ancestor for the angiosperms are not lessened under any other concept of angiosperm phylogeny to which I have been exposed; instead they are magnified to the point of desperation. Here again we see that the available information imposes severe limitations on the range of concepts which can be seriously entertained. The fact that under the Randalian concept we do have a possible ancestor for the angiosperms is one more piece of the theory that fits the other pieces, thus increasing our confidence that the theory is basically sound.

If I may be permitted one more digression, I should point out that when I speak of modern thinking, or a consensus, I am not unaware that it is easy to mistake one's own thoughts for the mainstream of opinion. There is certainly no lack of papers expressing ideas contrary to what I conceive to be the general opinion about angiosperm evolution. The recently published gonophyll theory (9) of Melville is an example. I do not accept the gonophyll theory, and I do not believe that most other taxonomists do. One of my friends commented, in referring to this and another novel interpretation of floral morphology, that "Carpels and stamens can be seen; gonophylls have to be imagined; and anthocorms offend the imagination." The paper I am presenting here is a mosaic and partial blend of my personal opinion and an attempt to assess the general opinion; I hope it is fairly plain which is which, or at least which I conceive to be which.

It is now generally agreed that the angiosperms are probably derived eventually from the seed ferns. The evidence for this conclusion has been presented by Takhtajan (10), among others. All other groups that have been suggested as possible ancestors can be ruled out on seemingly adequate grounds.

The *Chlamydospermae* (*Gnetales*, sens. lat.) were once taken seriously as possible ancestors of the angiosperms, and indeed *Gnetum gnemon* could pass for *Coffaea arabica* when in sterile condition, but the reproductive morphology of the *Chlamydospermae* is all wrong for a potential ancestor of the angiosperms (especially under the Randalian concept), and the idea has been generally abandoned. Even the gnetalean vessel, once seen as a possible link to the angiosperms, is now seen as a conclusive barrier to any such relationship. Bailey (11) and others have pointed out that the vessels in the *Gnetales* evidently originated from tracheids of the coniferophyte type with circular bordered pits, quite different from the fernlike (and cycadlike) scalariform tracheids that gave rise to the angiosperm vessel.

Even the seed ferns present some difficulties as possible ancestors to the angiosperms. It is now coming to be believed, on the comparative morphology of the angiosperms themselves, that the primitive position of the angiosperm ovule is on the upper (adaxial) surface of the carpel, instead of on the margins as was once believed. In the seed ferns the ovules were generally marginal or on the lower

(abaxial) surface of the leaves, but at least one seed fern, *Emplectopteris* (12) is generally interpreted as having the ovules on the upper surface, so perhaps there is no problem here after all. It is still a long ways, morphologically, from any known seed fern to any known angiosperm, but, unlike all other groups of gymnosperms, the seed ferns have the characters from which those of the angiosperms could logically have been derived. If anything should turn up to rule out the seed ferns as possible ancestors, then I suppose the angiosperms will have to hang on an evolutionary skyhook until more evidence is available or old evidence is reinterpreted.

PRIMITIVE CHARACTERS AND EVOLUTIONARY TRENDS

Nearly all modern systems of angiosperms fall into the deCandolle (13)—Bentham and Hooker (14)—Bessey (15) tradition that the Ranalian complex is primitive and that aggregation, fusion, reduction, and loss of parts are prominent trends in floral evolution. This is what we referred to earlier as the Ranalian concept of evolution. It is further generally agreed that the ancestral home of the angiosperms is in the moist tropics, that the woody habit is primitive, and that vessels have evolved from tracheids several times independently within the angiosperms. Inasmuch as *Austrobaileya* has a gymnospermous type of phloem (16), without companion cells and with scattered sieve areas rather than a terminal sieve plate on the sieve elements, it also appears that typical sieve tubes and companion cells evolved after the angiosperms had already differentiated from their gymnospermous ancestors.

The characteristic angiosperm stamen, with slender filament and terminal anther, evidently evolved in several parallel lines within the angiosperms from a broad, flat, sessile microsporophyll with sporangia embedded in the blade. This primitive type of stamen still exists in *Degeneria*, and stages in the evolution of the typical stamen from it are shown in various members of the Ranalian complex.

Even the closed carpel, which we customarily think of as definitive of the angiosperms, evidently originated several times among the primitive members of the group (17). Some species of *Drimys*, in the family *Winteraceae*, a member of the Ranalian complex, have thin, unsealed carpels that are merely folded along the midrib, the ovules being borne on the two inner surfaces of the folded carpel. The carpels of some species of *Bubbia* (*Winteraceae*), and of *Degeneria*, are very much like the *Drimys* carpels mentioned above, except for being abaxially somewhat deformed. In these genera a mat of tangled hairs running the length of the carpel serves as an elongate stigma on which the pollen grains germinate. Stages in the development of the typical simple pistil, with closed ovary, style, and terminal stigma are still preserved among various living members of the Ranalian complex.

It thus appears that vessels, true sieve tubes, companion cells, the angiospermous stamen, and the closed carpel, all of which are considered as typical angiospermous features, arose *within* the angiosperms. Furthermore, each of them arose several times in a series of more or less closely related parallel evolutionary lines, and in any one line they did not all evolve at the same time. Thus *Degeneria* has unsealed carpels and laminar stamens, but also has vessels, sieve tubes, and

companion cells; *Austrobaileya* has vessels and closed carpels, but lacks sieve tubes and companion cells; *Drimys* has unsealed carpels and lacks vessels, but does have sieve tubes and companion cells. Other combinations of ancestral and typical angiospermous characters occur in other members of the Ranalian complex.

Three features remain as characters which are largely or wholly restricted to angiosperms and which are uniformly developed in primitive members as well as in most or all of the more advanced members of the group. These are 1) germination of the pollen at some distance from the ovule; 2) the extreme reduction of the female gametophyte; and 3) double fertilization, with the attendant development (or at least initiation) of a triploid or polyploid endosperm. This last character fails in certain orchids (18), and of course in many apomicts in various families, but these exceptions are obviously special cases which have no bearing on the evolutionary history of the angiosperms as a whole.

It would be rash to assume that these three characters, on whose evolutionary history we have so little evidence, arose in any different phyletic pattern from the characters previously discussed. Double fertilization and the extreme reduction of the female gametophyte are probably phyletically linked, but the linkage need not have been a tight one. Reduction of the gametophyte is a general trend throughout the vascular plants, and further stages in the reduction of the female gametophyte, beyond the typical 8-nucleate stage, are to be seen within the angiosperms in various families which are not very closely related to each other. It seems likely that the evolution of the 8-nucleate embryo sac from the ancestral multicellular female gametophyte followed a similar pattern of parallelism.

Germination of the pollen grain at a point removed from the ovule is restricted to angiosperms, among living plants, but it also occurred in the fossil *Caytoniales*. This character is obviously correlated with the enclosure of the ovules, so that the pollen cannot land at the micropyle. Since we have seen that the evolution of the closed carpel occurred in a series of parallel lines, it seems reasonable to assume that pollen germination followed a similar evolutionary pattern.

Thus it appears that there probably never was an original angiosperm, from which all other angiosperms are descended. Rather we must visualize an evolving group of pteridosperms which broke up into a number of more or less parallel lines in which similar sets of evolutionary changes took place in only loose correlation with each other. There was no inherent point in time or morphological change at which we could say that *now and only now* the group has become angiospermous. The boundary must instead be arbitrary, and wherever this arbitrary boundary of angiospermy may be established, the several lines probably did not all cross it at precisely the same time.

Simpson, with abundant fossil evidence to back up the comparison of living species, has visualized a similar pattern for the origin of mammals (19). There was no original mammal, from which all other mammals are descended. Before one can trace all the mammals back to a common ancestor, one has not a mammal but a reptile. All the phylads which evolved from reptiles into mammals came from the same general taxonomic part of the reptiles, however, and there was a loose correlation in time as well.

I have elsewhere (20) pointed out that this sort of parallelism is a rather general evolutionary pattern, and that our taxonomic thinking should be adjusted to provide for it. Taxonomy can provide only a somewhat muddy reflection of phylogeny. The phyletic concept, and the monophyletic requirement for a natural taxonomic group, are useful and indeed necessary to a proper taxonomic system, but the monophyletic requirement must be interpreted broadly or it will get us into a lot of unnecessary trouble. In order to be natural and taxonomically acceptable, it is only necessary that a group fall somewhere toward the monophyletic end of the continuous scale which connects the strictest monophyly with the most utter polyphyly. Simpson (19) has proposed the useful rule of thumb that if all the members of a group of a given taxonomic rank are derived from another group of lesser taxonomic rank, that is a sufficient degree of monophyly for taxonomic purposes. The decision as to whether a proposed group is sufficiently monophyletic to be taxonomically acceptable will frequently require the exercise of personal judgment, but the necessity for such judgments is no stranger to taxonomy; indeed they cannot be avoided.

Parallelism is conspicuous at all taxonomic levels within the angiosperms, as well as being thoroughly involved in their origin. All of the common characters or specializations, and most of the rare ones, have arisen independently more than once, most of them several or many times, so that the occurrence of a particular character in two different families provides no guarantee of their close relationship. Even such a rare character as entomophagy has evidently arisen quite separately in the *Sarraceniales* and the *Lentibulariaceae*. One of the most frequent statements in Takhtajan's excellent review (21) of the evolutionary trends in individual characters of angiosperms is something to the effect that "this change has taken place repeatedly in the most diverse groups." Perhaps the most important weakness of Bessey's system (15) is that he failed to recognize how often perigyny and epigyny have arisen from hypogyny. The devastating error in Hutchinson's system (22, 23) is his assumption that there was an early and fundamental dichotomy between woody and herbaceous angiosperms.

This all-pervasive parallelism is indeed the chief obstacle to the formulation of a satisfactory general system. Just when the perception of a series of similarities between two groups leads us to postulate a close relationship between them, something else turns up to suggest that they are not so closely related and that the similarities are due to parallelism. I have pointed out elsewhere (20) that parallelism itself provides some evidence of relationship, because it reflects the realization of initially similar mutative and evolutionary potentialities, but the complex set of overlapping parallelisms in the angiosperms is difficult to understand and easily gives rise to conflicting interpretations. In establishing our concepts of relationships, we are going to have to pay more attention to what Thorne (24) has called non-missing links. It is the more primitive members of a group which give the best clues to its ancestry.

Another common problem in angiosperm taxonomy is that the characters marking the major groups, at the level of family and order, are usually difficult or impossible to correlate with ecologic niches and survival value. Most modern

students of evolutionary theory maintain that the correlations must exist, even if they are difficult to demonstrate; they cannot conceive of evolutionary trends or taxonomic groups that are not shaped primarily by selection, although they admit that the frequency of a particular mutation will differ in different groups. I have (20, 25) expressed the contrary opinion that evolution at the familial and ordinal levels in angiosperms is to a large extent shaped by the supply of mutations rather than by natural selection, and that many of the taxonomically important characters by which the families and orders are recognized have little or no selective significance. Regardless of who is right about this, the fact remains that no systematic attempt to find and elucidate such correlations for the Englerian or any other comprehensive system has come to my attention. The makers of systems have proceeded as if most of the families and orders of angiosperms had no selective significance; so far as the printed record shows, they have simply ignored the question.

Still another very serious obstacle to the development of a satisfactory general system is that the characters which mark the families and orders are subject to frequent exception. Exceptions to the ordinal characters are indeed so numerous that it is difficult to find criteria sufficiently stable for even the most loose and general characterization of the groups. Some botanists have gone so far as to say that the orders of angiosperms can be defined only by the list of families to be included. This may be an unnecessarily pessimistic position, but it does point up the difficulty.

The difficulty in characterizing families and orders may well be related to the seeming (or actual) lack of close correlation of many of the families and orders with well defined ecologic niches. If the taxonomically critical characters are not of great importance to the organism, or if the evolutionary barriers between different ecologic niches are minimal, then happenstance mutations affecting the critical characters will not be rigorously selected against. Differences in the corolla, for example, are very useful in characterizing the families and orders, yet many of the larger families have apetalous genera or species.

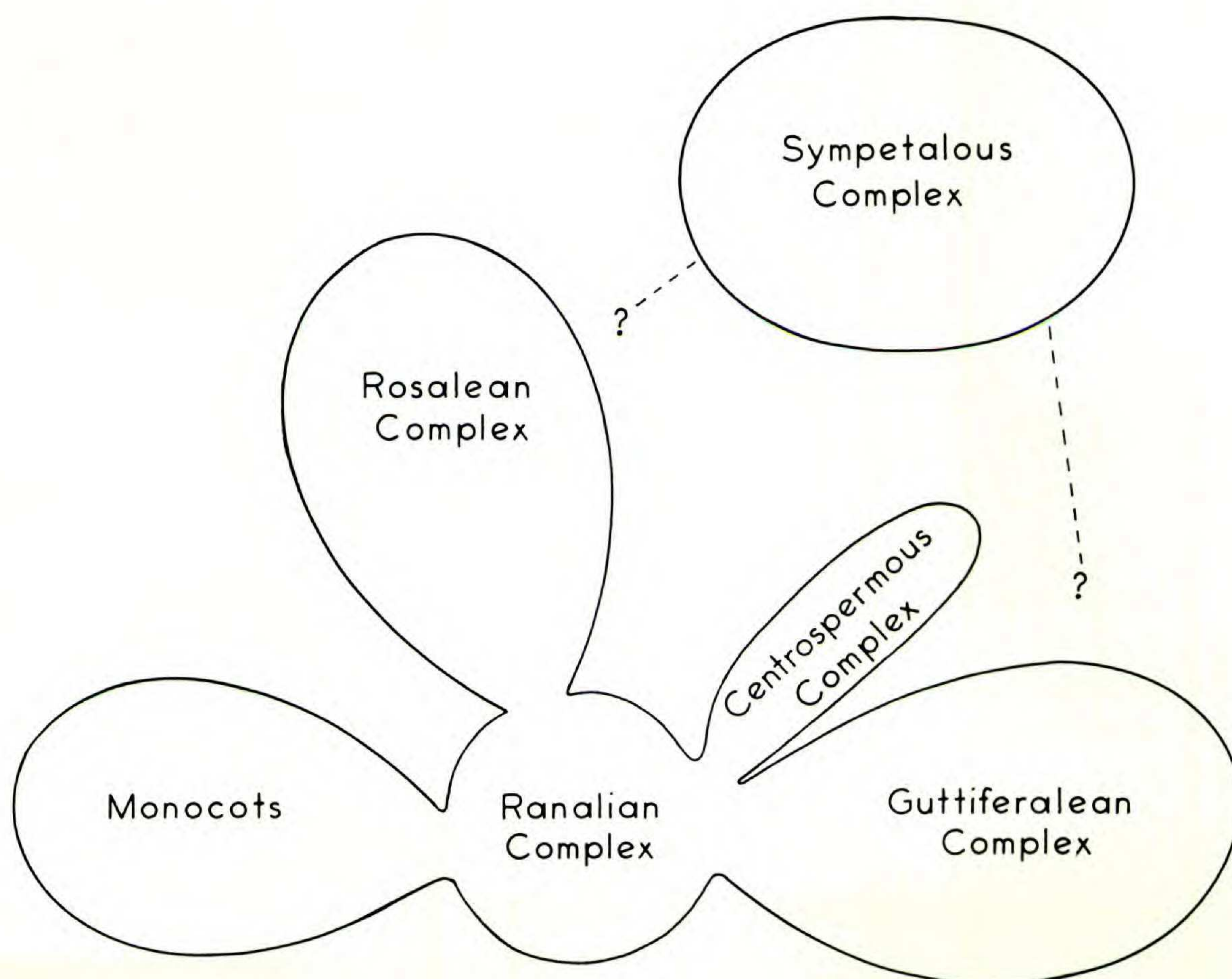
In spite of the difficulties, real progress is being made. We have already noted that any acceptable new system must fall within the deCandolle—Bentham & Hooker—Bessey tradition and must be largely shaped by what we have called the Ralian concept of angiosperm evolution. There is also a fairly general agreement on a number of the particular features in which such a system must differ from the traditional Englerian system.

As we have noted, there is a very large measure of agreement on how the genera of angiosperms should be assorted into families. A few problematical genera are kicked around from one family to another, and of course we will always have the problem of splitting versus lumping, but no one feels the need for a wholesale reshuffling of genera into families of different limitations constituted on different grounds. Changes in our concepts of families during the present century have been relatively minor. The current Engler Syllabus, to which we have already referred, is as good a standard for family limits as any, and it has the merit of providing a full description for each family.

The arrangement of families into orders, and the concepts of relationships among the orders, are as unsettled and controversial as the arrangement of genera into families is stable. Within the limits of what we have called the Rananian concept of angiosperm evolution there is still room for a great variety of systems, and it may yet be some time before a generally acceptable complete system emerges. Hutchinson's system of monocotyledons (22, 23) is very respectable, although I would prefer to see the families and orders more broadly defined. Hutchinson's scheme of dicotyledons, on the other hand, is hopeless, the most recent version (23) even more so than the earlier one (22) because now he has more nearly followed through the implications of his assumption that there was an early and fundamental dichotomy between woody and herbaceous angiosperms. Several years ago I published an outline scheme for the dicotyledons (26), to which I still adhere for the most part, although there are some things that need to be changed. Probably the best complete system which attempts to provide for all the families of both monocots and dicots is that of Takhtajan (21), but I believe it is still in need of substantial modification. I am looking forward to seeing the system that Thorne is working on, but I know little about what will be in it.

DICOTYLEDONS

A rough general idea of the probable relationships among the major groups of dicots may be had by visualizing two major and several minor lines of development from the Rananian complex. One major line leads to the *Guttiferales* (with the



Dilleniaceae as a connecting link), and thence to the *Violales* (*Parietales*), *Malvales*, *Ericales*, and *Ebenales*. In this line the stamens usually (always?) develop in centrifugal sequence, if there are enough stamens for any sequence to appear. The *Caryophyllales* (*Centrospermae*) and their allies likewise have centrifugal stamens and may be a basal branch from this line, or they may be a separate minor line of their own from the Ranalian plexus. The second major line from the *Ranales* leads to the *Rosales* and thence to such mainly compound-leaved groups as the *Sapindales*, *Geraniales*, and *Umbellales*. Several simple-leaved groups such as the *Myrtales*, *Celastrales*, *Linales*, *Polygalales*, and *Cornales* also relate to the rosalean line. In this line the stamens are always, so far as known, centripetal. A third large group consists of the orders *Gentianales* (*Contortae*) through *Asterales* in the Englerian sequence, with the exception of the *Cucurbitales*, which relate to the *Violales*. The affinities of this third group, which includes most but not all of the traditional *Sympetalae*, are still doubtful, although they must of course be derived eventually from the Ranalian complex.

The possible taxonomic significance of centrifugal stamens was first pointed out by Corner (27). It is generally conceded that the centrifugal sequence is secondary, being derived from the standard centripetal sequence, but the centrifugal type occurs in *Drimys* (28), which on other grounds is among the more primitive genera of angiosperms. Aside from *Drimys*, all the groups known to have centrifugal stamens fall into only two circles of affinity, the Dillenialean-Guttiferalean-Parietalean-Malvalean complex, and the centrospermous complex, and we have noted the possibility that these two complexes are themselves closely related. Determining the sequence of maturation is not always easy, however; often it is necessary to make long-sections of unopened buds. We should not be surprised if further studies tend to blur what now seems to be a fairly clear pattern.

The *Canellaceae*, which have customarily been referred to the *Parietales* because of their compound ovary and parietal placentation, are now generally admitted to belong in the Ranalian complex, or to be derived directly from it, which amounts to the same thing in terms of phylogenetic relationships. This is one of the few families of dicots to be actually moved in the new Engler Syllabus, where it appears after the *Myristicaceae* in the order *Magnoliales*.

Hutchinson's suggestion (22) that the *Aristolochiaceae* are derived from something in the Ranalian complex has met with general approval. Here we have one of Thorne's nonmissing links: *Saruma*, in the *Aristolochiaceae*, has well developed petals as well as sepals, and has essentially free carpels.

It is now admitted by all that *Paeonia* does not properly belong in the *Ranunculaceae* and must be treated as a family by itself. The necessity to remove *Paeonia* from the *Ranunculaceae* was pointed out as long ago as 1908 by Worsdell (29), who based his conclusion largely on anatomical grounds. In 1941 Gregory (30) found *Paeonia* to be cytologically anomalous in the *Ranunculaceae*. In 1955 Hammond (31) was unable to relate *Paeonia* to anything in the *Ranunculaceae* by his serological tests, although he did find that *Hydrastis* and *Glaucidium*, whose position in the family has been questioned, reacted with some other members of the *Ranunculaceae*. In addition to its persistent, leathery sepals and prominent

disk, *Paeonia* differs morphologically from the *Ranunculaceae* in having centrifugal stamens.

It is becoming customary to associate the *Paeoniaceae* and *Crossosomataceae* with the *Dilleniaceae* in an order or suborder of their own. This was first suggested, so far as I know, by Camp (32) in 1950. It has been almost universally adopted since then, including in my own work, but I am not sure that the situation is as clear as the developing consensus would suggest. Camp's grouping is very probably correct, but I don't think of it as being one of the firmly established parts of the system.

The order *Rhoeadales* has seemed to be one of the more natural orders, but recently we have been seeing repeated suggestions that it should be divided into two: the *Papaverales*, containing only the *Papaveraceae* and *Fumariaceae*, and the *Capparidales*, containing the remaining families, i.e. the *Capparidaceae*, *Cruciferae*, *Resedaceae*, *Moringaceae*, and *Tovariaceae*. Biochemical (33) and serological (34) evidence both seem to support this separation. The *Papaverales* are then seen as derived directly from the Ranalian complex, whereas the *Capparidales* are regarded as more nearly allied to the *Guttiferales* or *Violales*. I am dragging my feet a little on this one, and I would particularly like to see a careful investigation of the *Tovariaceae*, which have endospermous seeds like the *Papaverales*, and which have the placentae so deeply intruded that the placentation at first appears to be axile. Meanwhile it will perhaps do no harm to recognize the two orders as distinct, even if it eventually turns out that they are more closely related than now appears.

The close relationship among the *Guttiferales*, *Violales*, *Malvales* and *Capparidales* is now generally admitted, as is the transitional position of the *Dilleniaceae*, which are obviously part of the Ranalian complex, and equally obviously allied to the *Guttiferales*. The cucurbits have also become noncontroversial, and in the new Engler Syllabus they are moved to a position adjacent to the *Violales*. The only remaining difference of opinion is whether they (the cucurbits) should be submerged in the *Violales* or maintained in a separate order which is considered to be closely related to and immediately derived from the *Violales*.

Some of the traditional *Sympetalae* appear to be derived from the *Guttiferales*. Most obvious among these are the *Ericales*, which include both sympetalous and polypetalous members, even in such a relatively homogeneous group as the *Monotropoideae*. The small families *Clethraceae* (*Ericales*) and *Cyrillaceae* (*Guttiferales*) are sometimes seen as forming a near-connection between the two orders, but the position of the *Cyrillaceae* themselves is not wholly agreed on. The new Engler Syllabus retains the *Cyrillaceae* in the *Celastrales*, while commenting on their probable relationship to the *Guttiferales* and *Ericales*. Even without the *Cyrillaceae*, the *Clethraceae* are a good bridge between the two orders. The relationship of the *Clethraceae* to the *Ericaceae* has been evident to all, but their generally morphology is also consistent with a placement in the *Guttiferales*, a position which is also suggested by the pollen (35) and the nectaries (36).

The *Empetraceae*, with distinct or no petals, are now widely admitted to be reduced relatives of the *Ericaceae*, which they closed resemble in appearance. The *Empetraceae* are another of the small list of dicot families which are moved to radi-

cally new positions in the new Engler Syllabus, where they are relegated to the *Ericales*.

The *Lennoaceae*, a small group of nongreen root-parasites, were formerly included in the *Ericales*. More recent studies (35, 37, 38) indicate a position near the *Hydrophyllaceae* and *Boraginaceae*, and this is another family which has actually been moved in the new Engler Syllabus.

The *Ebenales* are now generally believed to be derived from the *Guttiferales* (*Theales*), as postulated by Copeland (39), although the evidence may not be so strong here as it is for deriving the *Ericales* from the *Guttiferales*.

The *Caryophyllales* (*Centrospermae*) consist of a relatively homogeneous core of 9 families (*Phytolaccaceae*, *Nyctaginaceae*, *Aizoaceae*, *Portulacaceae*, *Basellaceae*, *Chenopodiaceae*, *Amaranthaceae*, *Molluginaceae*, *Caryophyllaceae*), plus some certain (*Cactaceae*) and possible (*Polygonaceae*, *Didiereaceae*, *Batidaceae*, *Thelygonaceae*) allies which are sometimes but not always included in the group. The core families have a series of embryological features in common, which have been enumerated in the new Engler Syllabus, among other places. Notable among these features are the massive nucellus which develops into a perisperm in the seed, the double integument with the inner one forming the micropyle, trinucleate pollen, and peripheral embryo which tends to curve around the perisperm. When the stamens are numerous, as in the *Aizoaceae* and some *Portulacaceae*, they are centrifugal. All of these 9 core families except the *Molluginaceae* and *Caryophyllaceae* have betacyanins (or in some members betaxanthins) as flower pigments, lacking anthocyanins and anthoxanthins.

The betacyanins, sometimes in the past referred to as nitrogenous anthocyanins, are a distinct chemical group of flower pigments, apparently wholly unrelated to the anthocyanins. Among closely related forms they are often replaced by the yellow betaxanthins. The structure of betaxanthins remains to be elucidated, but Mabry & Turner (40) have reasonably suggested that they may be chemically much like the betacyanins, just as the anthoxanthins are much like the anthocyanins. So far as is presently known, betacyanins and betaxanthins do not co-exist with anthocyanins or anthoxanthins in the same flower, or even in the same family; a family has one or the other type of pigment (or neither) in its flowers, but not both.

Betacyanins are presently known only from the first seven families here listed in the *Caryophyllales*, plus the *Cactaceae* and *Didiereaceae*. They have not been found in those members of the *Caryophyllaceae*, *Molluginaceae*, *Polygonaceae*, *Batidaceae*, and *Thelygonaceae* which have been investigated, nor have they been found in families other than those here mentioned. Mabry (41) has suggested that the *Centrospermae* be defined solely by the presence or absence of betacyanin (or betaxanthin) in the flowers, thus excluding the *Caryophyllaceae* and *Molluginaceae* and including the *Cactaceae* and *Didiereaceae*, but such a treatment would require us to ignore the rest of the evidence. One-character taxonomy, like a one-mouse experiment, is always suspect.

The close relationship of the relationship of the *Cactaceae* to the *Caryophyllales* is now well established, and this is another family which has been moved in the new Engler Syllabus. Evidence from embryology (38, 42), pollen

morphology (35), and general morphology, as well as the evidence from the chemistry of the flower pigments, supports this view. Whether the *Cactaceae* should actually be included in the *Caryophyllales* or treated as a separate but closely allied order is a matter on which opinions may legitimately differ. Buxbaum (43) has vigorously expounded the view that the *Cactaceae* should be included in the *Caryophyllales*, but I myself prefer to retain the order *Cactales*.

The affinities of the *Didiereaceae*, *Batidaceae*, and *Thelygonaceae* are still uncertain. Rauh and Reznik (44) believe there is hardly any room for doubt that the *Didiereaceae* must be referred to the *Centrospermae*, along with the *Cactaceae*. In addition to the pigmentation, they cite certain similarities in pollen morphology, and some successful experimental grafts of *Didiereaceae* to *Cactaceae* made by Rauh. The cross-graft might at first seem to be definitive, but surprising as it may seem, graft-compatibility bears little relation to genetic affinity. Successful cross-grafts between widely differing families have been reported, even a monocot on a dicot, although in that instance a vascular connection was not formed (45). The embryological characteristics of the *Didiereaceae* have not been fully reported, or if they have I have not found the report, but the family does differ from typical centrospermous families in lacking perisperm, the food being stored in the embryo instead. The floral morphology is also difficult to reconcile with that of the *Caryophyllales* or *Cactaceae*, being reminiscent of the *Sapindales* or the less specialized members of the *Euphorbiales* instead. Although the *Didiereaceae* may ultimately have to be included in the *Caryophyllales*, this disposition of the family should be viewed with some reserve at least until more evidence is available.

The position of the *Batidaceae* is also uncertain. In habit and inflorescence they suggest some of the *Chenopodiaceae*, but they have binucleate instead of trinucleate pollen (3), they lack perisperm as well as endosperm, and they also lack betacyanins (40). Other suggestions which have been made as to their possible relationships are also doubtful.

The *Thelygonaceae* resemble typical *Caryophyllales* in floral morphology and gross structure of the seeds, but they have only a single integument, they have endosperm instead of perisperm, and they lack betacyanins. Their affinity remains doubtful.

The *Polygonaceae* resemble the *Caryophyllales* in floral morphology, and some of them have the typical curved, peripheral embryo of the *Caryophyllales* (46) but the food storage tissue is endosperm instead of perisperm. The pollen is trinucleate, as in the *Caryophyllales* (47), and it also resembles that of some *Caryophyllales* in micromorphology. *Paronychia* and some other genera of the *Caryophyllaceae* have a reduced number of ovules (sometimes only one) and are habitually suggestive of *Polygonum*. Like the *Caryophyllaceae*, the *Polygonaceae* lack betacyanins. I personally believe the two families are fairly closely related, but not everybody agrees with me. If the *Polygonaceae* are not allied to the *Caryophyllales*, their position is uncertain.

The *Plumbaginaceae* are now generally conceded to be derived from the *Caryophyllales*, in spite of the fact that they have a straight embryo and well developed endosperm and lack betacyanins. These differences are surely as formidable

as those which have caused some botanists to question the relationship of the *Polygonaceae* to the *Caryophyllales*, but thorough study by Friedrich (48) has been generally accepted as demonstrating the ancestry of the *Plumbaginaceae* in the *Caryophyllales*. Friedrich goes so far as to include the *Plumbaginaceae* in the *Centrospermae* (*Caryophyllales*) a disposition with which most subsequent authors have not agreed, but his concepts of relationship have not been seriously challenged. All students now agree that the *Plumbaginaceae* are not closely allied to the *Primulales*, with which they have often been associated in the past.

The *Primulales* are a well defined order that seem to have their own origin among the *Polypetalae*, distinct from that of other sympetalous groups. It was at one time widely assumed that they might be derived from the *Caryophyllales*, as shown in Bessey's well known phylogenetic "cactus", but more recent opinion has tended to favor an origin in the *Guttiferales*. The free-central placentation, once seen as a strong link between the *Caryophyllales* and the *Primulales*, is now regarded as more likely a result of parallel evolution. The *Myrsinaceae*, which belong to the order *Primulales*, are tropical and woody, and presumably the ancestors of the *Primulales* as a whole should be sought among the tropical, woody groups. The *Phytolaccaceae*, of the *Caryophyllales*, do have some tropical, woody members, but these have axile rather than free-central placentation. The few other tropical, woody members of the *Caryophyllales* are too specialized in other respects to be regarded as ancestral or near-ancestral to the *Primulales*. It would therefore appear that any possible phyletic connection between the *Caryophyllales* and the *Primulales* must have antedated the development of free-central placentation in both groups. Here we have an example of the danger of postulating the ancestry of a group on the basis of the advanced members instead of the primitive ones.

The traditional *Amentiferae* consist of diverse types with reduced flowers, rather than a coherent natural group. Several of the amentiferous families, including the *Moraceae*, *Fagaceae*, *Betulaceae*, and *Casuarinaceae*, are probably related eventually to the *Rosales* through something like the *Hamamelidaceae* (49, 50).² Others clearly belong elsewhere. The *Garryaceae* are now generally admitted to be derived from the *Cornaceae* (51). The *Juglandaceae* and *Julianaceae* are probably related to the *Anacardiaceae*, the *Julianaceae* (52) more certainly so than the *Juglandaceae* (53). The *Salicaceae* may be allied to something in the *Violales*, such as the *Flacourtiaceae*; in any case they have nothing to do with the other amentiferous families. As we have noted, the *Batidaceae* may or may not be allied to the *Caryophyllales*.

The *Podostemaceae* and *Hydrostachyaceae*, two small families of aquatics with reduced flowers, are now usually considered to be allied to the *Rosales* (sens. lat.), and several authors, including Hutchinson, Takhtajan, and myself treat the two families as making up a single order *Podostemales*.

The *Rosales*, sens. lat., are a large and diverse group of families held together more by their evident relationship than by a set of formal characters. Here we do

² Conversations with Armen Takhtajan in August, 1965 have made me receptive to the view that the *Hamamelidaceae* and their amentiferous allies may be derived directly from the Ranalian complex instead of through the *Rosales*.

approach the unfortunate condition of having an order defined by the list of families included. The diversity within the group has led some students to carve out several smaller orders, such as the *Cunoniales*, *Crassulales*, *Fabales*, *Hamamelidales*, *Pittosporales* and *Saxifragales*, but some of these are also difficult to define morphologically, and others consist only of one or a very few families. For purposes of further discussion the *Rosales* are here considered in the broad sense.

The *Rosales* are generally admitted to be derived from the Ranalian complex and to have given rise to several other groups. The *Podostemales* and some of the *Amentiferae* have already been mentioned as rosalean derivatives. The *Myrtales* are also generally conceded to be of rosalean origin, as is the large group of families that has been variously organized into the orders *Geraniales*, *Sapindales*, *Rutales*, *Polygalales*, and *Linales*. The number of orders to be recognized in this group, and which families to refer to which, are however still subject to considerable disagreement. The *Celastrales* and *Rhamnales* are also generally admitted to be derived from the *Rosales*, either directly or via the *Geraniales-Sapindales* complex.

The *Santalales* are generally admitted to be related to the *Celastrales*, but authors still differ as to whether they are derived directly from the *Celastrales*, or whether the two are initially parallel developments from the *Rosales*. In either case an eventual rosalean ancestry is indicated. Beginning with the *Olacaceae*, the *Santalales* show every transition from complete autotrophism through partial parasitism to complete parasitism. The nongreen family *Balanophoraceae* has traditionally been treated as a distinct order, but its relationship to the chlorophyllous members of the *Santalales* has been thoroughly demonstrated (54) and is now generally accepted.

The families *Rafflesiaceae*, *Hydnoraceae* and *Mitrastemonaceae*, which are intimately related among themselves, may or may not be properly referable to the *Santalales*. Traditionally they have been referred to the *Aristolochiales*, and this disposition of them has been maintained without significant comment by both Hutchinson and Takhtajan, but I find it difficult to accept. In my own opinion they are most at home in the *Santalales*.

Opinions differ as to the possible relationships of the *Umbellales* and *Cornales* to each other and to other orders, but in any case an eventual rosalean origin for both orders is indicated. In my own opinion the *Umbellales* and *Cornales* are not very closely related to each other. The *Umbellales* relate to the large group of mainly tropical trees, mostly with compound leaves, that I have referred to the order *Sapindales*. (Some of these are referred by other authors to the *Geraniales* instead). If the *Araliaceae* had the ovary superior instead of inferior, they would themselves fit nicely into this complex. The evolutionary progression from the *Araliaceae* to the *Umbelliferae* is admitted by all. The *Cornales*, on the other hand, are probably derived directly from the *Rosales*.

It is now admitted by all that the traditional *Sympetalae* are not a natural group. The probable affinities of the *Cucurbitales*, *Ebenales*, *Ericales*, *Primulales* and *Plumbaginales* have already been individually discussed. Once these orders have been disposed of, the rest of the *Sympetalae* pretty well hang together, so well, in fact, that it is often difficult to delimit the families. Aside from the general

morphological similarity and the transitional genera, the group is also held together by commonly having tenuinucellate ovules with a massive single integument. Unfortunately, the origin of the group is as obscure as its homogeneity is clear. The *Guttiferales*, the *Rosales*, and some things which I take to be derivatives of the *Rosales* (*Linales*, *Celastrales*, *Sapindales*) have been suggested as possible ancestors. I have not yet been able to reach an opinion on the ancestry of the group.

It has been customary to associate the *Rubiaceae* with the *Caprifoliaceae*, *Adoxaceae*, *Valerianaceae* and *Dipsacaceae* in an order *Rubiales*. There has been a current of unrest, however, in recent years about the true affinities of part or all of the *Caprifoliaceae*. *Sambucus* and *Viburnum*, in particular, are somewhat isolated within the family, and some people have speculated that one or both of them might be of a wholly different affinity. The external similarity of *Viburnum* to *Hydrangea* is obvious to anybody, but whether it reflects a real relationship is another question. I am inclined to doubt it. Now Wagenitz, in the new Engler Syllabus, has removed the *Rubiaceae* from the other families of the order (now called *Dipsacales*) and inserted the family (*Rubiaceae*) in the *Gentianales* as a near relative of the *Loganiaceae*. I have no doubt that the *Rubiaceae* are related to the *Loganiaceae*, and indeed there are two genera (*Gaertnera* and *Pagamea*) which are commonly referred to the *Rubiaceae* because of their evident relationships, but which have a superior ovary and have sometimes therefore been referred to the *Loganiaceae* instead. I do not see the need, however, to deny one relationship in affirming the other. So far as the presently available evidence is concerned, I do not see why there might not be an evolutionary line from the *Loganiaceae* through the *Rubiaceae* to the *Caprifoliaceae* and thence to the other families of the *Rubiales* (or *Dipsacales*).

The position of the *Adoxaceae* as relatives of the *Caprifoliaceae* and *Valerianaceae* has sometimes been questioned, with an affinity to the *Saxifragaceae* or some other polypetalous group being suggested instead. The traditional placement of the family receives strong support, however, from serological studies (55) which show an affinity between *Adoxa* and the *Rubiales*. The experiments showed a reaction between *Adoxa* and each of several members of the *Rubiales*, and with nothing else.

The *Callitrichaceae* are a group of aquatics with reduced, apetalous flowers. They have traditionally been referred to the *Geraniales*, where they have no obvious relatives. More recently it has become customary to associate them with the *Labiatae* and *Verbenaceae*, partly on the basis of embryological features (56). I was reluctant to take this step in my 1957 paper on the families and order of dicots, but I have been converted. This is another of the families that has been moved in the new Engler Syllabus.

I would like to be able to say that the relationships of the *Compositae* are now generally agreed upon, but unfortunately that is not so. Several years ago (57) I presented my reasons for believing them to be derived from the *Rubiales* rather than the *Campanulales*. I am still of the same opinion. Not everybody goes along with me, however, and the relationships of the *Compositae* are still controversial, even if not (in my opinion) doubtful.

Aside from the families which we are sure must be moved from their place in the traditional Englerian system, and others which can probably or surely be allowed to stay in or near their accustomed place, there are a number of families whose affinities are still controversial or uncertain. Among these, in addition to some we have already mentioned, are the *Coriariaceae*, *Elaeagnaceae*, *Euphorbiaceae*, *Krameriaceae*, *Pandaceae* and *Proteaceae*. I have an opinion on each of these, the opinion varying in strength and certitude according to the group, but some people differ with me. It remains to be seen how long it will take for a consensus to be reached.

MONOCOTYLEDONS

It is universally agreed that the monocots are derived from primitive dicots, and that the monocots must therefore follow rather than precede the dicots in any proper linear sequence. The dissected stele, the herbaceous habit, the absence of intrafascicular cambium, and the monocotyledonous embryo are all seen as secondary rather than primitive characters in the angiosperms as a whole, and any plant which was more primitive than the monocots in these several respects would certainly be a dicot. The monocots are more primitive than the bulk of the dicots in mostly having monocolpate pollen (rather than tricolpate or some other type), but several of the Ranalian families also have monocolpate pollen, so there is no problem here.

For the last several decades it has been customary to think of the *Helobiae* (*Alismatales* in the broad sense) as the most primitive monocots, and to see some sort of ancestral connection from these to the dicots via such things as the *Nymphaeaceae* and *Ranunculaceae*. I think there is something in this idea, and certainly the flowers of some of the *Helobiae* are more primitive than those of other monocots in having numerous stamens and numerous spirally arranged separate pistils. The situation is more complex than appears on the surface, however. Mature seeds of the *Helobiae* uniformly lack endosperm, and in this respect they are more advanced than a great many other monocots. The *Helobiae*, or at least those members which have been examined (47), have trinucleate pollen, an advanced character shared by few other groups of monocots. If the Helobian concept of monocot evolution is to be accepted at all, we must postulate an ancestor which differed from the modern *Helobiae* in having binucleate pollen and endospermous seeds. (I continue to use the term *Helobiae* in this discussion instead of the nomenclaturally preferable *Alismatales* because the latter name has often been used in a more restricted sense.)

A more serious challenge to deriving the monocots from the vicinity of the *Nymphaeaceae* has been posed by Cheadle (58, 59), who on the basis of comparative anatomical studies sees the monocotyledonous vessel as originating wholly independently of the dicotyledonous vessel. He therefore believes that any connection between the monocots and dicots must be between the primitively vessel-less members of the groups. The *Ranunculaceae* have well developed vessels. The *Nymphaeaceae* lack vessels, but the anatomy suggests to Cheadle and others that the absence of vessels from this group is secondary rather than primitive. (However, it

may be worth noting that Takhtajan (10) considers the *Nymphaeaceae* to be primitively vessel-less.) The only vessel-less monocots so far known are aquatics—the *Lemnaceae* and certain members of the *Helobiae* (but not the *Alismataceae*). Cheadle sees nothing in any of these vessel-less monocots to suggest that any of their ancestors ever had vessels, and he feels that such an ancestry should not be lightly postulated. However, the *Lemnaceae* are on other grounds clearly to be considered as reduced derivatives from the *Araceae*, which have vessels in the roots. *Pistia*, a free-floating, aquatic, pantropical genus, is a good example of an aroid which points toward the *Lemnaceae*.

A full exposition of the matter would take more time than we have available here today, but I see no reason why the entry into an aquatic habitat by the ancestors of the present monocots might not have led to a partial or complete loss of vessels, and a cutting off of later stages in ontogeny so that only a “primitive” type of xylem was produced. To give a rough analogy, we know that the loss of a single gene can break an important biosynthetic chain in snapdragons, preventing the formation of the typical zygomorphic corolla and kicking the corolla back to the more primitive, regular form. Something similar may have happened to the xylem of the early monocots, in the absence of any selective pressure to maintain the more advanced structure. Then when descendents of these aquatic plants returned to a terrestrial habitat, a more advanced xylem structure was again developed under selective pressure.

The reason that I cling to the Helobian concept of monocot evolution is that if we abandon it, or if we deny any possible connection between the early monocots and such groups as the *Ranunculaceae* and *Nymphaeaceae*, then we create much greater obstacles to the development of a reasonable scheme than we avoid. An exploration of these problems will not be undertaken here and now; we don’t have time.

An aquatic origin for the monocots provides a possible explanation for the nature of the typical monocot leaf: it is a phyllode, essentially a flattened petiole with the blade suppressed. This morphological interpretation was proposed as long ago as 1827 by deCandolle (60) and was further elaborated by Arber (61) in 1925. The transformation of a normal-looking leaf with blade and petiole to a typical monocot leaf with parallel venation can be seen under appropriate circumstances in *Sagittaria*. I was very much impressed to see all stages between the two extremes in a single population of a species of *Sagittaria* some years ago in northern Minnesota. In shallow water near the shore of the pond the leaves had normal blades and petioles. In somewhat deeper water the petiole was thinner and more flattened, and the blade was more or less reduced. In still deeper water the leaf was wholly submersed and consisted only of the flattened, thin, parallel-veined petiole, a perfectly normal monocot leaf. There was also some variation on the leaves of an individual plant, the first-formed leaves often being smaller, wholly submerged, and bladeless, whereas the later-formed ones were larger and had vestigial or more or less well developed aerial blade. This same environmentally controlled dimorphism in *Sagittaria* was reported by deCandolle.

It may well be that the leaf blade in *Sagittaria* is itself merely an expanded

petiole-tip, phylogenetically distinct from the leaf blades of dicotyledons, and that the now essentially palmate venation of some species of *Sagittaria* has been derived within the family from parallel venation, but the present structure is nonetheless that of a petiolate leaf with a well defined, palmately veined blade. It is perfectly clear that *Sagittaria* plants with the genetic potentiality to produce normal leaves can be induced to develop instead typical monocotyledonous parallel-veined leaves which are really flattened petioles. Genetic (and eventual evolutionary) fixation of a character which first appeared as a direct response to the environment is amply provided for in modern evolutionary theory (62).

Whether the interpretation that fits *Sagittaria* can be extended to the whole class *Monocotyledonae* is of course another question. I believe it can and should be so extended, and Arber gives a detailed exposition in support of this view. Under this concept terrestrial monocots with well defined, net-veined blade are considered to be derived from ancestors with narrow, parallel-veined leaves without a well defined blade, and indeed all transitional stages are seen in several families, such as the *Araceae*. An attempt to read the series the other way means that we must start with dicot-type leaves in diverse groups of monocots having nothing to do with each other, and have these all converge in both floral and vegetative characters into a hopelessly polyphyletic core of typical monocots. The resulting system, if it could be called that, would be shot full of internal contradictions.

Within the monocots, it is now clear to everybody that the *Cyperaceae*, *Gramineae*, *Sparganiaceae* and *Typhaceae* have reduced rather than primitive flowers. The *Typhaceae* and *Sparganiaceae* are closely related inter se, but they have nothing to do with the *Cyperaceae* and *Gramineae*. The relations of the order *Typhales* (including only the *Typhaceae* and *Sparganiaceae*) are obscure; perhaps they are derived eventually from something in the *Liliales*.

Among the followers of the Randalian and Helobian school of thought it has been fairly customary to think of the *Cyperaceae* and *Gramineae* as progressively reduced types of Lilialean ancestry, with the *Juncaceae* as a sort of half-way house between the *Liliaceae* and *Cyperaceae*. This still appears to be sound at least as far as the *Cyperaceae* are concerned. In addition to the traditional characters, the discovery of the so-called diffuse centromere in both the *Cyperaceae* and *Juncaceae* (63, 64) tends to strengthen the concept that the two families are closely related. On the other hand, there is a growing current of opinion that the grasses may not be closely allied to the *Cyperaceae*. The two families are so similar in so many respects that I am reluctant to give up the thought that they are closely allied, but a mounting list of authors has felt it necessary to treat each of the two families as a monotypic order, and both Takhtajan (21) and Potzal (65) have treated the *Graminales* as being allied to the *Flagellariaceae*—*Restionaceae*—*Centrolepidaceae* cluster of families and not to the *Liliales*. On the other hand, Hutchinson (23) thinks that the *Restionaceae* and *Centrolepidaceae* are allied to the *Juncaceae*, and Koyama (66) sees the *Cyperaceae* as being allied to the *Restionaceae*, so that a relationship of the grasses to the *Restionaceae* and *Centrolepidaceae* would not be incompatible with a relationship also to the *Cyperaceae*. I want to look further into this matter before expressing an opinion.

A final point with regard to the monocots is that it is now abundantly clear that the traditional distinction between the *Liliaceae* and *Amaryllidaceae* on the basis of superior vs. inferior ovary is unnatural and must be abandoned. Inferior ovaries have been derived from superior ovaries several times in different groups of lilies. *Yucca*, with the ovary superior, is obviously related to *Agave*, with the ovary inferior, and these and several other genera are now generally admitted to be more closely allied among themselves than any of them are to the traditional *Liliaceae* or *Amaryllidaceae*. It is now becoming customary to recognize the *Agavaceae* (including *Yucca*) as a distinct family, and to recognize several other families in the *Liliaceae*-*Amaryllidaceae* complex as well. The number and limits of these families are not yet agreed on, but Hutchinson's attempt to use the inflorescence instead of the position of the ovary as the critical character has not been widely accepted. This would put *Allium*, for example, in the *Amaryllidaceae* instead of in the *Liliaceae*. I would have been just as happy to expand the limits of the *Liliaceae* to include the traditional *Amaryllidaceae*, instead of trying to recognize several families, but I have sometimes been accused of being a lumpner anyway.

SUMMARY

It is now generally believed that the angiosperms were probably derived from seed ferns. This belief is based on the fact that all other groups can apparently be excluded on adequate grounds, whereas the seed ferns do have the characters from which those of the angiosperms could logically have been derived. The fossil record provides but little assistance in clarifying the ancestry of the angiosperms or their relationships inter se, but it does suggest that woody angiosperms antedate herbaceous ones; herbs do not become a prominent part of the fossil record until the beginning of the Miocene period, whereas woody groups extend back at least to the Cretaceous.

The familiar and useful Englerian system of angiosperms is now moribund, largely because it fails to recognize the significance of reduction and therefore tends to equate the simple with the primitive. With due allowance for the differences between splitters and lumpers, most of the Englerian families can stand with little or no change, but the arrangement of families into orders, and especially the concepts of relationships among the orders, must be largely recast.

Three factors combine to make the formulation of a satisfactory new system very difficult: (1) The all-pervasive parallelism within the group; (2) the seeming (or real?) lack of correlation of most of the characters marking the major groups with ecologic niches and survival value; and (3) the numerous exceptions to the characters which mark the major groups. This is about the situation one might expect if evolution at the familial and ordinal levels in angiosperms were governed largely by the supply of mutations rather than by natural selection. However, most present-day students of evolutionary theory cannot conceive of evolutionary trends or taxonomic groups that are not shaped primarily by selection, with the supply of mutations merely imposing limits on what selection can do.

No complete system which provides for all the families has yet gained general

acceptance as the successor to the Englerian system, but it is widely agreed that any acceptable new system must fall within the limits of what may be called the Rananian concept of angiosperm evolution. Under this concept the Rananian complex is considered to be primitive, and aggregation, fusion, reduction, and loss of parts are considered to be prominent trends in floral evolution.

Within the dicotyledons, the Rananian complex gave rise to two major evolutionary lines (here called the Rosalean complex and the Guttiferalean complex) and several minor ones. The centrospermous complex may be a basal branch from the Guttiferalean complex, or it may be more directly derived from the Rananian complex. The traditional *Amentiferae* consist of several different groups which have independently achieved the amentiferous condition. Most of these probably relate in one way or another to the Rosalean complex, but the *Salicales* are probably derived from the Guttiferalean complex (via the "Parietales") instead, and the *Batidales* may or may not be related to the centrospermous complex. A large proportion (but not all) of the traditional *Sympetalae* form a closely knit group whose immediate ancestry is obscure, although they must be derived eventually from the Rananian complex.

The monocots are evidently derived from primitive dicots (i.e. from the Rananian complex), perhaps originally as a group of aquatics more or less similar to the modern *Helobiae*, but with endospermous seeds. The typical monocot leaf with parallel venation probably represents a flattened petiole with the blade suppressed; monocots with well defined, net-veined blades probably have monocot ancestors with typical monocot leaves. The traditional distinction between the *Liliaceae* and *Amaryllidaceae* on the basis of superior or inferior ovary is unnatural and must be abandoned. Such families as the *Typhaceae*, *Gramineae*, and *Cyperaceae* are florally reduced rather than primitive.

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